ON THE HYBRID NATURE OF *QUERCUS BASASEACHICENSIS* (FAGACEAE, SECT. *QUERCUS*)

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ABSTRACT

Quercus basaseachicenis C. H. Muller, collected by LeSueur in 1936 and named by Muller in 1938, was not recollected until 1985. Since that time this white oak (sect. *Quercus*) has been discovered at several sites in the Sierra Madre Occidental in Chihuahua and extreme northern Durango, Mexico. For the first time fruiting material is described. *Quercus basaseachicensis* occurs with two other white oaks, the low, shrubby, rhizomatous *Q. depressipes* Trel. and the robust shrub or tree *Q. rugosa* Née, and is intermediate between them. Evidence based on habitat, habit, leaf morphology (including pubescence) is presented to indicate the hybrid nature of *Q. basaseachicensis*. The name *Q.* ×*basaseachicensis* C. H. Muller, pro sp., is proposed.

RESUMEN

Quercus basaseachicensis C. H. Muller, que fue colectado por LeSueur en el año 1936 y descrito por Muller en 1938, no ha sido vuelto a recolectado hasta 1985. Desde entonces este roble blanco (secc. *Quercus*) ha sido encontrado en algunos lugares en la Sierra Madre Occidental de Chihuahua y en el norte extremo de Durango, México. Se describen por el primer vez plantas con flores y frutos. *Quercus basaseachicensis* convive con dos otros robles blancos muy diferentes, uno el pequeño, arbusto, rizomatoso *Q. depressipes* Trel., el otro el arbóreo o arbusto grande, *Q. rugosa* Née, siendo intermedio entre los dos. Se presentan evidencias basadas en el hábitat, hábito, morfología y indumento de las hojas para indicar la naturaleza hibrida de *Q. basaseachicensis*. Se propone el nombre *Q.* ×*basaseachicensis* C. H. Muller, pro sp.

INTRODUCTION

Harde LeSueur, from the University of Texas, was the first botanist to collect at what is presently the Parque Nacional "Cascada de Basaseachic" on the west slope of the Sierra Madre Occidental in southwestern Chihuahua, approximately 300 air km. W of Cd. Chihuahua. Among the extensive collections he made in 1936 was a peculiar white oak, which C. H. Muller named *Quercus basaseachicensis* in 1938. LeSeuer's specimens were vegetative and Muller's new species, therefore, necessarily lacked descriptions of flowers and fruit. Nevertheless, on leaf morphology alone Muller placed the new species in the subgenus *Leucobalanus* Engelm. (= subg. *Quercus*) and, with excellent insight, in the series *Reticulatae* Trelease. Muller

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noted that a study of the fruit would probably remove the species from this section, to which he felt it was only distantly related. He also noted that "at present there exists no other series to which the species could be referred, and its characters are not sufficiently plain to serve as the basis of a new series." With no additional information, Camus (1938-39) and Martínez (1956) followed Muller's classification of *Q. basaseachicensis* exactly.

Nearly 50 years passed before this oak was collected again. In 1985, during general floristic collecting at Basaseachic, and in subsequent years of botanical exploration in the northern Sierra Madre Occidental, I and associated collectors discovered about 20 plants referable to *Q. basaseachicensis* (Fig. 1 and Appendix). A few of these were in flower or in fruit. This paper, then, reports upon these collections, provides a description of habit of the plant and its flowers and fruits, and provides morphological and ecological evidence that *Q. basaseachicensis* is a rarely formed hybrid, which at Basaseachic at least shows some segregration or backcrossing to the parental types. A plant closely resembling the isotype was determined to have $2n=24$ chromosomes (Rodriguez & Spellenberg 1992), the usual number in *Quercus*.

The parental species are believed to be the extensively rhizomatous *Q. depressipes* Trel., a patch-forming low shrub, and the robust shrub or tree *Q. rugosa* Née, two distantly related white oaks placed in different series (Trelease 1924; Camus 1938-39; Martínez 1956). This paper follows Nixon's (1993) infrageneric classification. He also notes that those oaks such as *Q. depressipes*, which are from Mexico and the southwestern United States and have connate cotyledons, form the *Glaucoideae* and probably are distinct at the subsectional level from those with free cotyledons, but a classification has yet to be devised. The hybrid between these very different white oaks that is under consideration here has not been observed to form self-perpetuating populations, and for this reason the hybrid name *Q.* ×*basaseachicensis* C. H. Muller, *pro sp.*, is proposed (basionym: *Q. basaseachicensis* C. H. Muller. 1938. Amer. Midl. Naturalist 19:582; Type: Mexico: Chihuahua, Cascada de Basaseachic, 6 Jul 1936, *LeSueur 549*; holotype: Muller's pers. herb., transferred to BH; isotype: TEX! [photo at NMC]).

ADDITIONS TO DESCRIPTION OF *QUERCUS* ×*BASASEACHICENSIS*

Shrubs 1–1.8 m tall, few to many stemmed, rarely rather extensively rhizomatous and forming patches up to ca. 5 m across. Staminate aments 15–42 mm long, with 4–20 flowers in the distal 80%, sparingly stellate tomentose; perianth sparingly to rather densely tomentose, 1.5 mm wide, about as long; anthers 3–7, glabrous, tan or reddish brown, 1.0–1.5 mm long. Pistillate flowers 1–4, in distal 1/3 of sparingly stellate pubescent to glabrate peduncle 15–41 mm long, usually only 1(–3) maturing. Cups

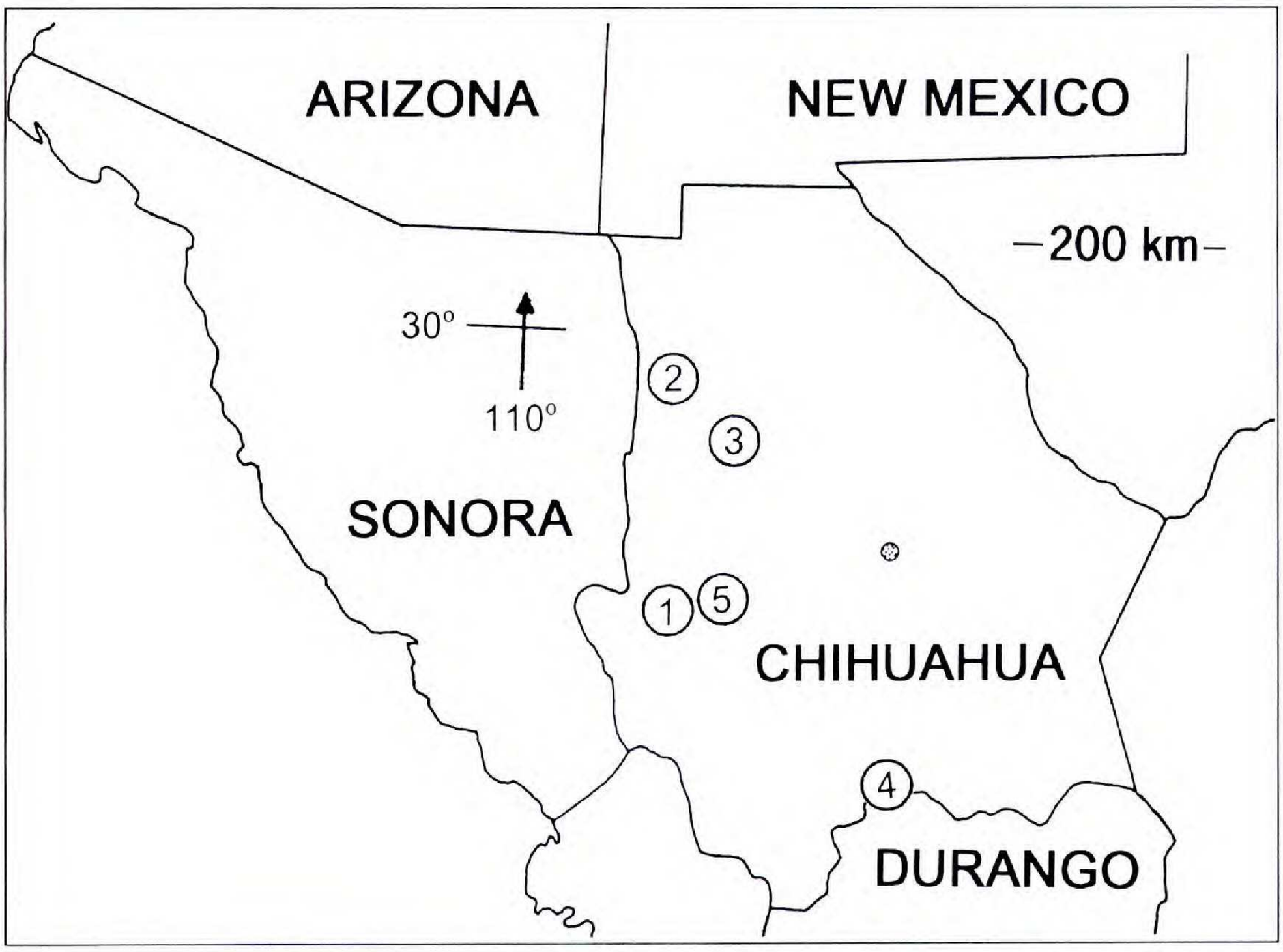


FIG. 1. Locations in the northern Sierra Madre Occidental, northwestern Mexico, of *Quercus* ×*basaseachicensis*. Numbered circles correspond to sites described in Appendix and following. Site 1, Chihuahua, Municipio Ocampo, Parque Nacional "Cascada de Basaseachic," the type locality. Site 2, Chih., Mcpio. Casas Grandes, 14.4 road km E of Altamirano. Site 3, Chih., Mcpio. I. Zaragoza, 1.1 km E of pass over Sierra Catarina. Site 4, Dgo., Mcpio. Ocampo, 13 km W of crossing of Rio San Juan. Site 5, Chih., Mcpio. Guerrero, 14.4 road km W of Tomochic. The small shaded circle is the location of Cd. Chihuahua, given for reference.

hemispheric, 10–12 mm wide, 8–10 mm deep, the mature scales with reddish or brown densely appressed-pubescent bases, narrowed to thin, glabrate, reddish or tan, round or more or less acute tips that are puberulent on margins. Acorns ovoid, 11–12 mm long, 8–10 mm wide, light brown, about 1/2 included. Cotyledons pale pink, fused by their edges, separate in the center in the basal 2/3.

HYBRID NATURE OF *QUERCUS* ×*BASASEACHICENSIS*

Oaks are notorious for the frequency of hybridization within subgenera (see, for example, Stebbins 1950, pp. 61–66). Evidence for the hybrid nature of *Quercus* ×*basaseachicensis* is provided by the habitat and by macro- and micromorphological intermediacy. The hybrid is always uncommon. Presently *Q.* ×*basaseachicensis* is known from five sites (Fig. 1). In Sites 1–4 both putative parents are immediately sympatric; at Site 5 *Q.* ×*basaseachicensis*

grew immediately beneath *Q. rugosa*, but the nearest *Q. depressipes* (along the highway) was noted at ca. 1.5 km distant.

Habitat. —*Quercus depressipes* and *Q. rugosa* have about the same elevational range in Chihuahua and northern Durango, that is, ca. 1950–2600 m, the latter presently known to extend somewhat higher than the former. *Quercus* ×*basaseachicensis* occurs between 1980 and 2225 m. *Quercus rugosa* commonly occupies sites seeming to be more mesic, commonly in canyons, on north- or northeast-facing slopes, and often on deeper soils. *Quercus* depressipes commonly occurs on open sites, often on thin rocky soils.

As is virtually common knowledge, and as reviewed by Grant (1981, p. 199 ff.), hybrid plants are particularly common in disturbed areas. At Basaseachic (Site 1 in Fig. 1) 12 putative hybrid plants have been located, all along the trail leading from the parking lot to the top of the falls. In this area, *Q. rugosa* is common, *Q. depressipes* is rare. At Basaseachic *Q. depressipes* is common on open rocky slopes with little tree cover, but in the forested area where *Q. basaseachicensis* plants occur *Q. depressipes* is not frequent. It may have been more common here in the past, and is now succumbing to succession after fire (pines in the area are ca.125 years old or younger, and bases of many large *Cupressus* are fire-scarred). Where it occurs in the Sierra Madre, *Q. depressipes* may increase very rapidly in open areas generated by fire (R. Corral D., pers. comm). One intermediate at Basaseachic, a few-stemmed shrub about 1.2 m tall near the top of the stairs where the trail crosses the Río Basaseachic, very closely resembles the isotype (TEX) (Fig. 2) in macromorphology and in the characteristics of the pubescence on the abaxial surface of the leaf (Figs. 4, 6) (in the various collections made during this study, this plant has been designated plant "#2"). No plants referable to *Q.* ×*basaseachicensis* have been found in other areas of the park even after 10 years of general collecting there to detail the flora. At Basaseachic the range of variation in hybrid plants suggests that some are either backcrosses to the parental types, or are later-generation segregates (Fig. 2); at the other sites only more or less exact intermdeiates (F_1s?) are present. All of the plants at Basaseachic are few-stemmed shrubs; none are extensively rhizomatous.

At the northernmost site (Fig. 1, Site 2) two plants referable to *Q.* ×*basaseachicensis* were found where both *Q. depressipes* and *Q. rugosa* are common. Intermediate plants occurred only near the edges of a dirt road. Both intermediate plants were few-stemmed non-rhizomatous shrubs.

In the Sierra Catarina (Fig. 1, Site 3), six plants referable to *Q.* ×*basaseachicensis* occur along a sharply defined contact between *Q. depressipes*, which forms an extensive and continuous patch across the open east face of a hillside, and *Q. rugosa*, which is the dominant tree (also shrub) on the north-facing slopes of a narrow canyon (cf. Boecklen & Spellenberg 1990

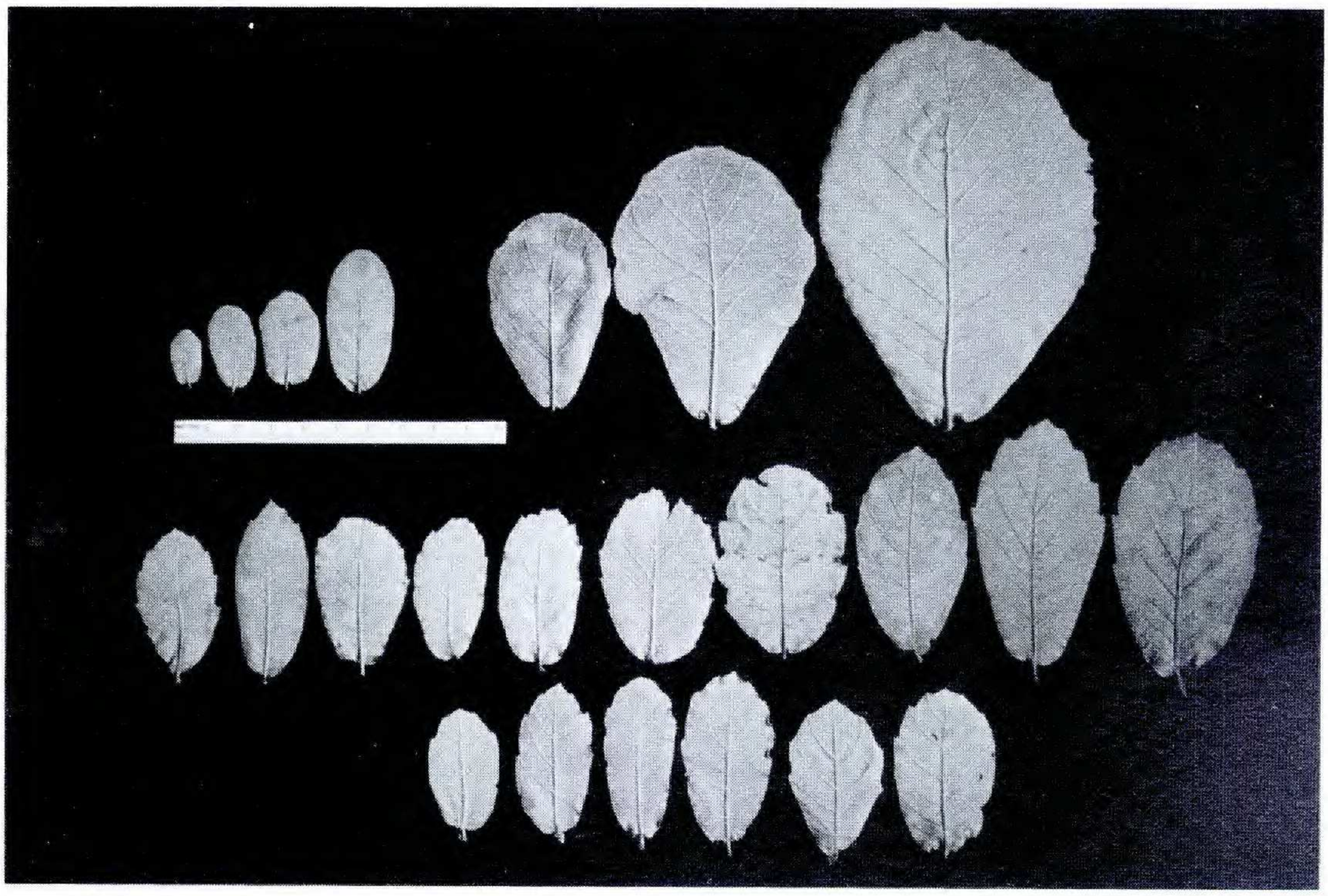


FIG. 2. Comparison of leaves from *Quercus* depressipes, *Q. rugosa*, and putative hybrids. Plants are referenced by collection number; number following hyphen signifies individual plant in population (which is indicated in voucher specimens). See Appendix for locations. Top row, group of four leaves at left, *Q. depressipes* (3 at left from *9589*, right leaf from *8919-6*). Top row, right, group of three leaves, *Q. rugosa* (2 at left from *10038*, right leaf from *11834*). Middle row, *Q.* ×*basaseachicensis* from Basaseachic (l-r, *8919-8, 8919-6, 9341-2* [possibly from type plant], *10042-4*, *LeSueur 549* [isotype, TEX], *10042-9, 8974-1, 8989-7, 9588-3, 8919-5*). Bottom row, Q. ×*basaseachicensis* from the Sierra Catarina (l-r, *9739-4, 8955-1, 8955-2, 9739-6, 8213-5, 9739-3*). White scale is 10 cm long.

for a more extensive description of this site). Intermediate plants do not occur outside this line of contact. One of these intermediates is extensively rhizomatous, forming a thick patch several meters in diameter. Another four or five intermediate plants occur in a canyon ca. 1/2 km to the northeast where *Q. rugosa* and *Q. depressipes* are intermixed.

Macro- and Micromorphological Comparisons.—Hybrids in oaks are commonly detected by macromorphological intermediacy, particularly by characteristics of the leaves (e.g., Bartlett 1951; Benson, Phillips & Wilder 1967; Cottam, Tucker & Santamour 1982; Hardin 1975; Stebbins, Matzke & Epling 1947; Tucker 1961). In Table 1 several macro- and micromorphological features of *Quercus* depressipes, *Q. rugosa*, and *Q.* ×*basaseachicensis* are compared. Intermediacy of putative hybrids between *Q. rugosa* and *Q. depressipes* in leaf size and shape was demonstrated by multivariate methods for plants in the Sierra Catarina (Site 3) (Boecklen & Spellenberg 1990), and is evident for two populations in Fig. 2.

Even a casual examination of the abaxial surface of the leaf reveals con-

spicuous differences between the species, and intermediacy in many of the characters by *Quercus ×basaseachicensis*. With a dissecting microscope *Quercus rugosa* is seen to be prominently bullate and minutely papillate (due to the prominently convex surfaces of the epidermal cells), *Q. ×basaseachicensis* less so, and *Q. depressipes* not at all bullate, and with the cell surfaces only obscurely convex. The bullate vs. non-bullate nature of the abaxial surface is evident in Figs. 3–5, as are the differences in the convexity of the cells.

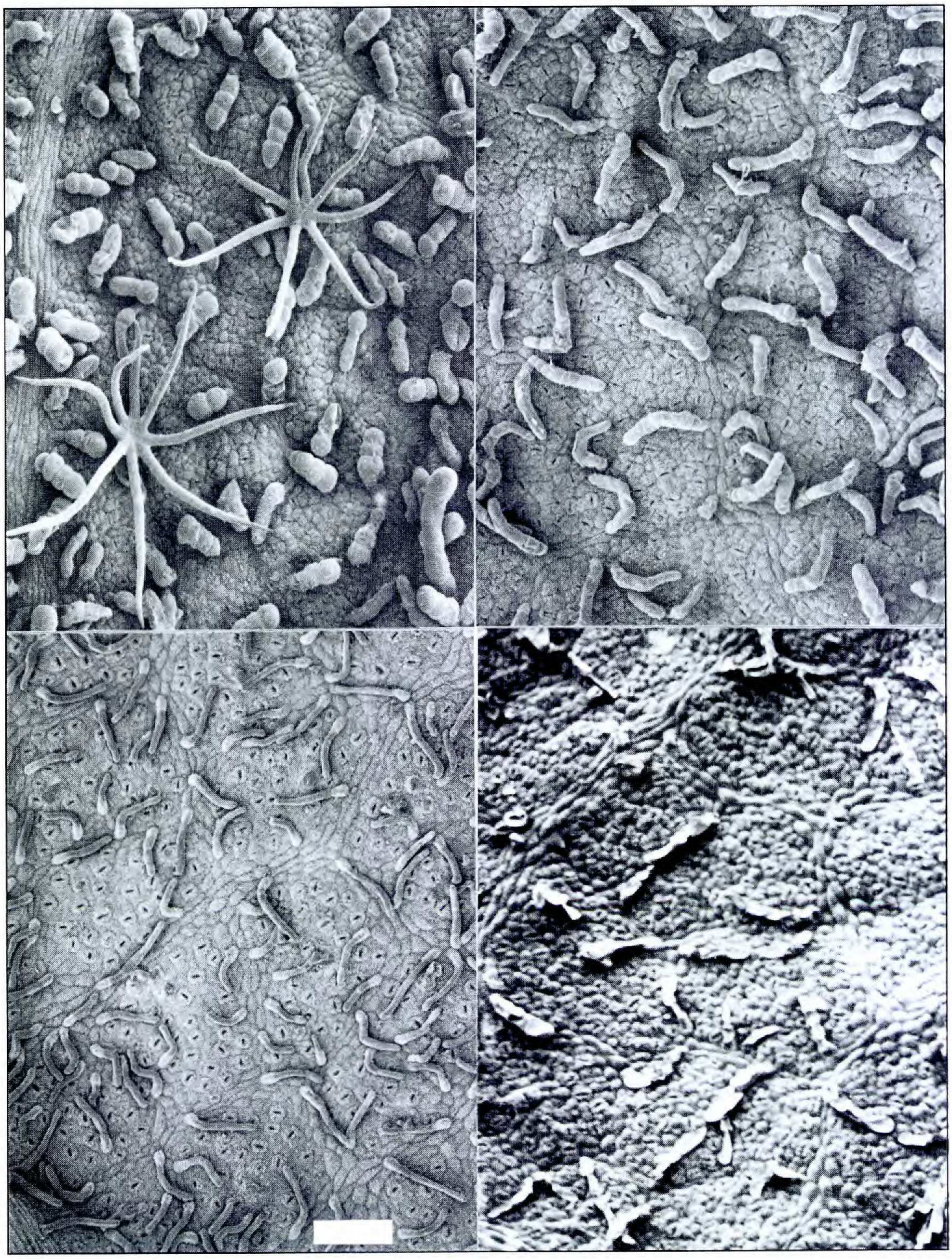
Several authors have shown that characteristics of the indumentum are important in distinguishing oak taxa (e.g., Hardin 1979; Manos 1993; Nixon & Steele 1981; Thomson & Mohlenbrock 1979) and useful in the detection of hybrids (Cottam, Tucker & Santamour (1982). To more critically examine and illustrate features of the indumentum of the abaxial leaf surface, specimens were examined with scanning electron microscopes (ETEC Autoscan 500 at University of New Mexico; Philips 501B at New Mexico State University). Fresh leaf tissue was fixed in FAA, dehydrated, critical point dried, sputter-coated with gold, and photographed at 80x. Material from the isotype was treated in the same manner.

Quercus rugosa has stellate hairs on the abaxial leaf surface (Fig. 3), whereas *Q. depressipes* does not (Fig. 5). The isotype of Q. *×basaseachicensis* also lacks stellate hairs (Fig. 6), as do most of the plants believed to be hybrids at Basaseachic (Fig. 4). In the Sierra Catarina (Site 3) some intermediates have stellate hairs, others do not. Intermediate plants from sites 2, 4, and 5 all lack stellate hairs.

The species and the intermediates, including the isotype, also differ in the size of a second type of foliar trichome, the small, gold or white vermiform hairs on the abaxial surface of the leaf. Those of *Quercus rugosa* are large, easily seen, and often coalesce in age into dark droplets. The hairs are sufficiently small in *Q. depressipes* that even under a hand lens the leaf must be well lit for one to detect their presence. The hairs differ in length and diameter between *Q. rugosa* and *Q. depressipes* (Table 1), with those of *Q. ×basaseachicensis* being intermediate.

CONCLUSION

The comparison of very different kinds of characters made in Table 1 differs little from the character count procedure described by Wilson (1992) and indicates that *Q. ×basaseachicensis* probably is, in fact, a hybrid between the very different white oaks *Q. depressipes* and *Q. rugosa*. Hybrid plants are rare and always occur with one, and usually both, the putative parents. Based on leaf characteristics, including features of the indumentum, the plant in Figure 4 (plant #2 in the various Basaseachic collections we have made) may actually be the type plant from which LeSueur collected in 1936. Admittedly, on habit and leaf characteristics it would be difficult at



3 ▶ ◀ 4

5 ▶ ◀ 6

FIGS. 3–6. Abaxial epidermis of white oaks from Basaseachic (white bar at base of Fig. 5 represents 100 microns). Fig. 3. *Quercus rugosa* (*#11838*), illustrating two stellate hairs and numerous large multicellular vermiform hairs. Fig. 4. *Quercus* ×*basaseachicensis* (*#11840*, plant 2), showing only middle-size vermiform hairs. Fig. 5. *Quercus* depressipes (*#11839*), showing only minute vermiform hairs. Fig. 6. *Quercus* ×*basaseachicensis* (*LeSueur 549*, TEX, isotype) showing only middle-size vermiform hairs (collapsed) similar in size and density to those in Fig. 4.

TABLE 1. Comparison of several macro- and micromorphological attributes of *Quercus depressipes*, *Q.* ×*basaseachicensis*, and *Q. rugosa*.

Attribute	Species of Oak		
	Q. depressipes	*Q.* ×*basaseachicensis*	*Q. rugosa*
HABIT	Shrub, often extensively rhizomatous (rarely not), forming large patches	Shrub, occasionally fairly rhizomatous, usually not	Tree, occasionally a non-rhizomatous shrub
HEIGHT	0.3–(2) m	1–3 m	(2)3–20 m
LF COLOR	pale bluish green	pale bluish green to deep green	deep, dark green
LF LENGTH	2–4 cm	4–7.5 cm	5–13 cm
LF WIDTH	1–2.3 cm	1.9–5.1 cm	3.8–10.0 cm
LF MARGIN	Entire, or with 1–3 teeth on each side near apex	Entire to toothed throughout	Usually irregularly toothed throughout, rarely subentire
ABAXIAL SURFACE, LF	Smooth, no veins impressed; smallest veinlets colored as areolae	Slightly rugulose the larger veins somewhat impressed; smallest veinlets somewhat paler than areolae	Rugulose, all but the smallest veins impressed; smallest veinlets notably paler than areolae
ABAXIAL EPIDERMIS, LF	Smooth, cells very slightly convex	From rather smooth and with cells slightly convex to rather bullate and cells strongly convex	Strongly bullate and microscopically papillate with cells strongly convex
PUBESCENCE, ABAXIAL SURFACE, LF	Appearing glabrous, but with very minute golden vermiform hairs; no stellate hairs	Minutely pubescent, with small golden vermiform hairs, some plants also with sparse stellate hairs	Noticeably pubescent, with large golden vermiform hairs and with stellate hairs
LENGTH, VERMIFORM HAIRS	0.05–0.13 mm	0.09–0.21 mm	0.13–0.33 mm
DIAMETER, VERMIFORM HAIRS	ca. 10 microns	ca. 20 microns	ca. 30 microns
FRUITING INFLORESCENCE	peduncle 0.7–2.5 cm, fruits 1–2 near tip, often only 1 maturing	peduncle 2–4 cm, fruits 1–4 in upper 30%, often only 1 maturing	peduncle (2)6–13 cm, fruits 1–7 in upper 60% most maturing
COTYLEDONS	connate (except in center near base); flesh white	connate at margins, center free; flesh pale pink	free; flesh deep pink

best to eliminate another common white oak, *Q. arizonica* Sarg., which occurs at Basaseachic sympatrically with *Q. rugosa*, as a parent instead of *Q. rugosa*. Characteristics of the pistillate inflorescence (Fig. 7) and the cotyledons provide insight. *Quercus* ×*basaseachicensis* has rather long peduncles in the pistillate inflorescence (Fig. 7), generally longer than those of *Q. depressipes* and shorter than those of *Q. rugosa* (Table 1). In *Q. arizonica* the

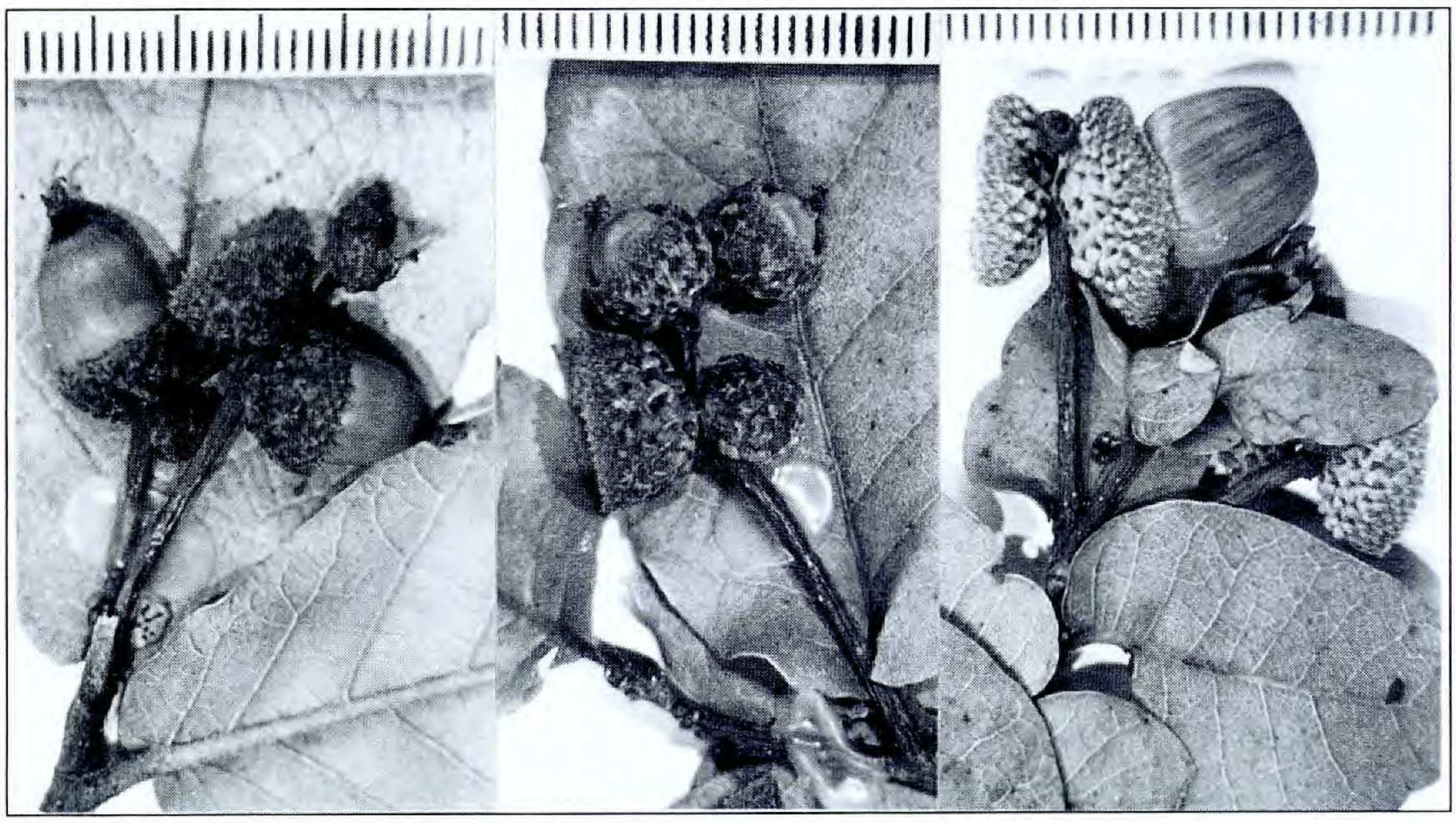


FIG. 7. Comparison of fruiting inflorescences of *Quercus rugosa* (*10038*) (left), *Q.* ×*basaseachicensis* (*9341-2*) (middle), *Q. depressipes* (*8598*) (right). Inflorescence from *Q. rugosa* is at short end of range of variation; that from *Q. depressipes* is from long end. Units of scale at right in mm. Photos from specimens at NMC. All specimens cited in appendix except that of *Q. depressipes*, which is: *Spellenberg & Zimmerman* 8598, Chihuahua, Mcpio. Bocoyna, S edge of village of Bocoyna, 12 Sep 1986.

peduncle rarely exceeds 11 mm in length. Plant #2 at Basaseachic has only partially connate cotyledons, as do several plants from the Sierra Catarina (Site 3). In *Q. arizonica* and *Q. depressipes* cotyledons are nearly or completely connate; in *Q. rugosa* they are distinct. At Site 3 *Q.* ×*basaseachicensis* occurs along a precise and very narrow line of contact between *Q. rugosa* and *Q. depressipes*, and west of Casas Grandes (Site 2) Q. ×*basaseachicensis* occurs where *Q. depressipes* and *Q. rugosa* are intermixed. In neither case is *Q.* ×*basaseachicensis* closely associated with *Q. arizonica.* At site 4, in northern Durango, *Q. arizonica* is also present and intermixed with *Q. rugosa* and *Q. depressipes*. At this site parentage of the intermediate is certainly open to question.

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APPENDIX

Specimens seen for this paper, with herbaria of deposition (CHIH = Univ. Autonoma de Chihuahua; ESAHE = Colegio de Graduados, Escuela Superior Agricultura "Hermanos Escobar" in Juarez [now closed; possibly to be transferred to Univ. Autonoma de Cd. Juarez]). Collection numbers are those of Spellenberg and various associates. Sites of collections are shown on Figure 1.

SITE 1—Chihuahua, Mcpio. Ocampo, Parque Nacional "Cascada de Basaseachic," 108°12'30"W, 28°10'N, elev. 1980 m, in association with various oaks and pines.

Q. basaseachicensis: *LeSueur* 549, 7-6-36 (TEX!, isotype); *8467*, 26 Apr 1985 (BH, DAV, CHIH, SAHE, NMC); *8794*, 4 Oct 1986 (NMC); *8919*, 16 Oct 1986 (NMC); *9341*, BH, IBUG, NMC, TEX); *9588*, 1 Aug 1988 (CAS, CIIDIR, IEB, NMC); *9638*, 1 Aug 1988 (NMC); *9660*, 2 Aug 1988 (ASU, MEXU, NMC, US); *10042*, 28 Oct 1989 (MEXU, UC); *10924*, 26 Sep 1991 (MEXU, MO, NMC, NY); *11840*, 17 Jun 1993 (BRIT, DAV, RSA)

Q. depressipes : *8469*, 27 Apr 1987 (MEXU); *8919*, 16 Oct 1986 (NMC); *9589*, 1 Aug 1988 (CAS, CIIDIR, IEB, NMC); *9643*-A, 1 Aug 1988 (NMC); *10799*, 25 Jun 1991 (F); *11839*, 7 Jun 1993 (NMC)

Q. rugosa: *8917*, 16 Oct 1986 (NMC); *9341*, 12 Sep 1987 (BH, BRIT, CAS, IEB, NMC); *9590*, 1 Aug 1988 (NMC, UC, US); *10038*, 28 Oct 1989 (CIIDIR, MEXU, NMC); *10926*, 26 Sep 1991 (NMC); *11838*, 17 Jun 1993 (F)

SITE 2—Chihuahua, Mcpio. Casas Grandes, 14.4 road km E of Altamirano, 43 km W of junction with Casas Grandes-7 Colonia Juárez road, ca. 108°40'W, 29°40'N, elev. 2225 m, in association with various oaks and pines.

Q. basaseachicensis: *9192*, 10 Jun 1987 (CIIDIR, DAV, MEXU, NMC)

Q. depressipes: *9191*, 10 Jun 1987 (CIIDIR, MEXU, NMC)

Q. rugosa: *9190*, 10 Jun 1987 (CIIDIR, MEXU, NMC)

SITE 3—Chihuahua, Mcpio. I. Zaragoza, 25 km SW of Buenaventura, 1.1 km E of pass over Sierra Catarina, 107°38'W, 29°46'N, elev. 2290 m, in association with various oaks and pines.

Q. basaseachicensis: *7956*, 8 Feb 1985 (DAV, MEXU, NMC); *8940*, 11 Nov 1986 (ENCB, MO); *8955*, 16 Nov 1986 (BRIT, COLO, DAV, F, NMC, RM, SRSC); *9213*, 18 Aug 1987, (ARIZ, CAS, CIIDIR, IBUG, MEXU, NMC, NY, UNM, US); *9738*, 23 Sep 1988 (BH, MEXU, NMC, NY); *9739*, 23 Sep 1988 (ASU, IEB, INIF, MT, NMC, RSA, TEX); *10936*, 12 Oct 1991 (GH)

Q. depressipes: *7955*, 8 Feb 1985 (MEXU, NMC); *10060*, 30 Oct 1989 ARIZ, BRIT, CAS, CIIDIR, MEXU NMC); *8941*, 14 Nov 1986 (BH, F, IEB); *9212*, 18 Aug 1987, (MEXU, NMC, NY); *9740*, 23 Sep 1988 (IBUG, NMC)

Q. rugosa: *8939*, 11 Nov 1986 (ASU, IBUG); *8954*, 16 Nov 1986 (COLO, DAV, F, IEB, INIF, NMC, NY, SRSC); *8956*, 16 Nov 1986 (MEXU, NMC); *10059*, 30 Oct 1989, (ARIZ, BRIT, CAS, CIIDIR, MEXU, NMC)

SITE 4—Durango, Mcpio. Ocampo, on road between Hidalgo de Parral and Guadalupe y Calvo, 13 km W of crossing of Río San Juan, 24 km E of El Vergel, 106°12'W, 26°40'N, elev. 2280 m, with various oaks and pines.

Q. basaseachicensis: *8543*, 12 Jul 1986 (CAS, CIIDIR, MEXU, NMC)

Q. depressipes: *8542*, 12 Jul 1986 (MEXU, NMC)

SITE 5—Chihuahua, Mcpio. Guerrero, 14.4 road km W of Tomochic, ca. 108°58'W, 28°21'N, elev. 1950 m, in association with various oaks and pines.

Q. basaseachicensis: *9660*, 2 Aug 1988 (ASU, MEXU, NMC, US)

Q. rugosa: *9659*, 2 Aug 1988 (NMC)

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